This is a digital copy of a book that was preserved for generations on library shelves before it was carefully scanned by Google as part of a project to make the world's books discoverable online.

It has survived long enough for the copyright to expire and the book to enter the public domain. A public domain book is one that was never subject to copyright or whose legal copyright term has expired. Whether a book is in the public domain may vary country to country. Public domain books are our gateways to the past, representing a wealth of history, culture and knowledge that's often difficult to discover.

Marks, notations and other marginalia present in the original volume will appear in this file - a reminder of this book's long journey from the publisher to a library and finally to you.

Usage guidelines

Google is proud to partner with libraries to digitize public domain materials and make them widely accessible. Public domain books belong to the public and we are merely their custodians. Nevertheless, this work is expensive, so in order to keep providing this resource, we have taken steps to prevent abuse by commercial parties, including placing technical restrictions on automated querying.

We also ask that you:

+ *Make non-commercial use of the files* We designed Google Book Search for use by individuals, and we request that you use these files for personal, non-commercial purposes.
+ *Refrain from automated querying* Do not send automated queries of any sort to Google's system: If you are conducting research on machine translation, optical character recognition or other areas where access to a large amount of text is helpful, please contact us. We encourage the use of public domain materials for these purposes and may be able to help.
+ *Maintain attribution* The Google "watermark" you see on each file is essential for informing people about this project and helping them find additional materials through Google Book Search. Please do not remove it.
+ *Keep it legal* Whatever your use, remember that you are responsible for ensuring that what you are doing is legal. Do not assume that just because we believe a book is in the public domain for users in the United States, that the work is also in the public domain for users in other countries. Whether a book is still in copyright varies from country to country, and we can't offer guidance on whether any specific use of any specific book is allowed. Please do not assume that a book's appearance in Google Book Search means it can be used in any manner anywhere in the world. Copyright infringement liability can be quite severe.

About Google Book Search

Google's mission is to organize the world's information and to make it universally accessible and useful. Google Book Search helps readers discover the world's books while helping authors and publishers reach new audiences. You can search through the full text of this book on the web at `http://books.google.com/`

QL
847
C47

[illegible]
2w 3

B 485778

Chapman. A Thesis

Science Library
QL
847
.C47

JAN 28 1919

The
Basal Connections of the Tracheae of the Wings of Insects

The Basal Connections of the Tracheae of the Wings of Insects

By ROYAL NORTON CHAPMAN, M.A.

A Thesis presented to the Faculty of the
Graduate School of Cornell University in
partial fulfillment of the requirement for
the degree of Doctor of Philosophy

(Reprinted from *The Wings of Insects* by John Henry Comstock)

Ithaca, N. Y.
The Comstock Publishing Company
1918

THE BASAL CONNECTIONS OF THE TRACHEÆ OF THE WINGS OF INSECTS

By ROYAL NORTON CHAPMAN, M.A.

THIS paper is the result of an investigation undertaken at the suggestion of Prof. J. H. Comstock, under whose direction the work has been done. The purpose of the work has been to determine the generalized type of the basal connections of the tracheæ of insect wings and to ascertain what the principal lines of modification have been, with the hope that the conditions of the basal connections of the tracheæ may offer some explanation for some of the modifications of the tracheæ in the wings themselves.

It was found by Comstock and Needham (*American Naturalist*, xxxii, 1898, p. 88–89) that the tracheæ that supply the wings with air arise from two distinct trunks, an anterior costo-radial trunk and a posterior cubito-anal trunk. In certain generalized insects these two trunks are distinct; where this condition exists the medial trunk is a member of the costo-radial group of tracheæ. In most insects there has been developed a transverse trachea connecting these two groups of tracheæ, the transverse basal trachea (Fig. 17, *tb*).[*] When a transverse basal trachea is formed, the base of the medial trachea tends to migrate along it towards the cubito-anal group of tracheæ, and often becomes united with that group.

Comstock and Needham were unable to explain the cause of the formation of a transverse basal trachea and the migration along it of the base of the medial trachea when it is formed. Concerning this they made the following statement: "It is probable that these changes have to do with improving the air supply of the wing; but we have not sufficient data, as yet, to warrant a definite statement on this point."

---

[*] LETTERING OF THE FIGURES ILLUSTRATING THE BASAL CONNECTIONS OF THE TRACHEÆ OF THE WINGS OF INSECTS.

a. c-r, accessory costo-radial trachea;
a. cu-a, accessory cubito-anal trachea;
a. dl, accessory longitudinal trachea;
as, anterior stem of the leg trachea;
c, costal trachea;
c-r, costo-radial trachea;
cu-a, cubito-anal trachea;
d. lt, dorsal longitudinal trachea;
g, tracheal gill;
gt, gill trachea;
l_2, mesothoracic leg trachea;
l_3, metathoracic leg trachea;
lt, longitudinal thoracic trachea;
mt, muscle trachea;
ps, posterior stem of the leg trachea;
r. sp_1, rudiment of the mesothoracic spiracle;
r. sp_2, rudiment of the metathoracic spiracle;
r. sp_3, rudiment of the first abdominal spiracle;
sp_1, mesothoracic spiracle;
sp_2, metathoracic spiracle;
sp_3, first abdominal spiracle;
sp_4, second abdominal spiracle;
tv, transverse basal trachea;
u, union of the costo-radial and transverse basal tracheæ;
vlt, ventral longitudinal trachea;
v. sp_2, vestige of the metathoracic spiracular trunk;
v. sp_3, vestige of the first abdominal spiracular trunk.

A desire on the part of Professor Comstock to have ascertained the exact nature of the basal connections of the tracheæ of the wings in different orders of insects, in the hope that this knowledge would throw light on this problem, led him to suggest the making of the investigation the results of which are given here.

Another condition that suggested the same question is the fact that in the Odonata the branches of the medial trachea invade the region of the tracheæ of the radial sector, which becomes greatly reduced. If the medial trachea has a better air supply than has the radial trachea, this invasion can be understood.

The references to the basal connections of the wing tracheæ which have been found in literature are few and fragmentary. So far as can be determined no general study of the subject has been made previously. However, various authors, while working on closely related subjects, have noted and described the conditions in certain forms. These descriptions may be best referred to in the parts of the paper relating to these various forms.

However the work of Karel Sulc [Über Respiration, Tracheensystem und Schaumproduction der Schaumcikadenlarven (Aphrophorinae-Homoptera) Zeitschrift für wissenschafliche Zoologie. 1911:99, p. 147–188] deserves special mention. This author described and figured the tracheal system of *Philaenus lineatus* L. with detailed drawings of the leg and wing tracheæ in the various nymphal stages. The basal connections of the wing tracheæ are more generalized than those of the Hemiptera described and figured in this paper (Figs. 22, 23, and 24) and agree with the typical condition of the wing tracheæ (Figs. 17a and 17b) except that the transverse basal trachea has been developed. The basal connections of the fore wing pad of a first stage nymph of *Aphrophora salicis* are described and figured in which the transverse basal trachea is not developed and the costo-radial and cubito-anal groups of tracheæ are shown arising respectively from the anterior and posterior stems of the leg tracheæ.

Careful dissection was found to be the best means of studying the tracheæ. The use of transmitted light to distinguish the opaque tracheæ in the more or less transparent bodies, without dissection, was not satisfactory because it was not possible, in this way, to accurately determine the relationships of the tracheæ which lie one above the other. Nymphs and pupæ were dissected under water and care was taken not to break large tracheæ and allow the air to escape. In this way the tracheæ were kept filled with air and were easily studied. Several dissections were made of each species and the results were carefully checked over to make sure that no tracheæ had been broken or overlooked.

The dissections were drawn with a camera-lucida before the air had escaped from the tracheæ and while the trunks retained their normal size. It is to be noted that no pretense has been made to include all of the muscle tracheæ; only the larger muscle tracheæ connected with the wing or leg tracheæ have been shown.

THE TYPICAL ARRANGEMENT OF THE BASAL CONNECTIONS OF THE TRACHEÆ OF THE WINGS

Two diagrams of what seems to be the typical condition of the basal connections of the wing tracheæ have been constructed (Fig. 17). The condition of the tracheal branches to the wings and legs, as figured in these diagrams, does not differ in any of its essentials from the condition found in the more generalized insects. It will also be noticed that none of the insects studied present conditions which cannot be looked upon as modifications of this typical condition. The construction of these diagrams is, therefore, necessary only to simplify the discussion of the modifications of the typical condition and not to represent an imaginary step in the development of any of the conditions found in any of the more specialized insects studied.

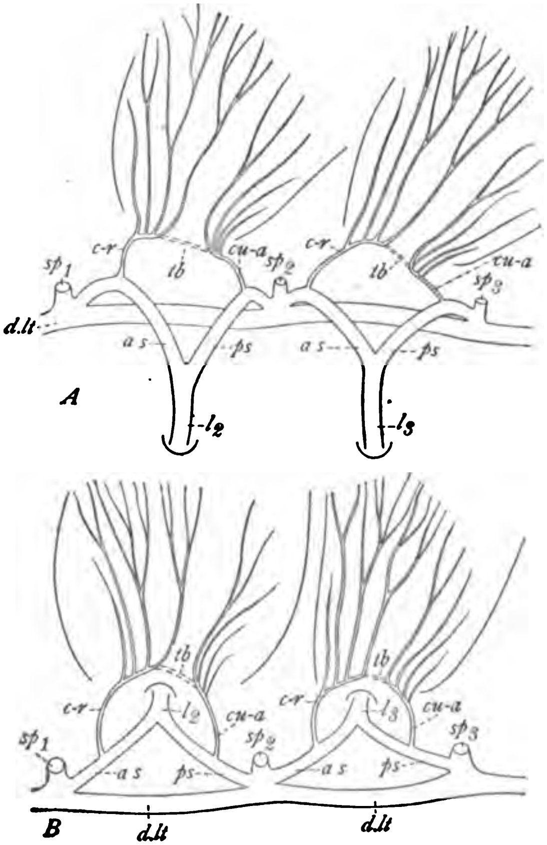

Fig. 17.—The typical condition of the basal connections of the tracheæ of the wings of insects. A. Side view. B. Dorsal view.

One of the diagrams (A) is a side view of the thoracic tracheæ in which the wing tracheæ are represented as extending vertically above the thorax and those of the legs extending downward. The other diagram (B) is a dorsal view of the thoracic tracheæ and represents the tracheæ of both the wings and legs extending laterad. It must be kept in mind that when the thorax is viewed from the dorsal side the wings are directly above the legs (Fig. 17, B). Since the conformation of some of the insects has made it necessary to draw the dissections from the side view and others from the dorsal view, the two diagrams are given to aid in the comparison of these two different aspects of the thorax.

There are three spiracles directly connected with the respiration of the wings; one in each of the last two segments of the thorax and one in the first segment of the abdomen (*sp*₁, *sp*₂, and *sp*₃). The anterior and posterior of these two spiracles (*sp*₁ and *sp*₃) each contributes one tracheal branch to the appendages of the mesothorax and the metathorax respectively. The middle spiracle (*sp*₂) contributes two branches; one to the mesothoracic appendages and one to the metathoracic appendages. In this way each wing and each leg receives two tracheal branches; one from the spiracle anterior to it (*c-r* to the wing, and *as* to the leg) and one from the spiracle posterior to it (*cu-a* to the wing, and *ps* to the leg.) This condition is retained, in its essentials, in all the insects studied. Even tho the metathoracic spiracle is absent in many of the more specialized insects, its position is indicated by the rudimentary spiracular trunk (Fig. 21, *r. sp*₂), from which arise branches to the thoracic appendages, very much as in the more generalized insects, where the metathoracic spiracle is well developed.

As has already been stated, these branches that arise from the trunks at the bases of the spiracles supply air to both the wings and the legs. The leg tracheæ are Y-shaped; each leg trachea being formed by the union of two trunks. These trunks are designated as the anterior stem (*as*) and the posterior stem (*ps*) respectively. In the more generalized insects the branches to the wings arise from the stems of the leg tracheæ, which form the arms of the Y. The figure of the nymphal cockroach (Fig. 18) shows that the tracheæ going to the legs are much larger than those leading to the wings. The relations of the leg and wing tracheæ are such that it seems very evident that the branches coming from the spiracles are primarily leg tracheæ and that the branches to the wings are secondary.

In some cases the wing and leg tracheæ arise separately from the spiracles. Such a condition may be explained as the result of a divergence of the bases of the two tracheæ which has been carried so far that their connections are entirely separate. However the more general relations between the tracheæ to the wings and those to the legs have been retained, at least to some extent, in all of the insects studied. For this reason it would seem that a consideration of the tracheæ to the wings cannot ignore the condition of the tracheæ to the legs. If there is any preference as to the air supply from the different spiracles which results in a modification of the tracheæ to the wings, some modification of the tracheæ to the legs might also be expected. If it is found that any factor causes changes in the tracheal branches to the wings, it may be expected that a similar factor affecting the legs will cause similar changes in the tracheæ entering the legs and the converse should also be true.

EXAMPLES OF THE MORE GENERALIZED ARRANGEMENT

The basal connections of the wing tracheæ in a cockroach nymph (Phylodromia germanica), Order Orthoptera.—The condition of the tracheæ in the cockroach is very similar to that shown in the diagrams. The connections are as shown in the drawing (Fig. 18) which is a dorsal view. The cubito-anal tracheæ (*cu-a*) originate nearer the spiracles than the costo-radial tracheæ (*c-r*) do, but they have the typical connections with the stems of the leg tracheæ (*as* and *ps*) which form the two arms of the Y-shaped leg tracheæ. There are muscle tracheæ (*mt*) which go to the coxal muscles but they do not continue into the legs as do the tracheæ labeled l_2 and l_3.

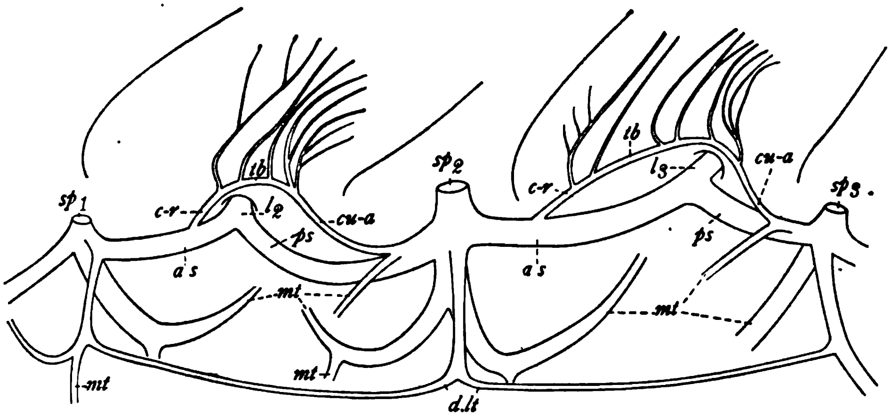

Fig. 18.—The basal connections of the wing tracheæ of a cockroach. Dorsal view.

In the nymphal cockroach there is a single slender dorsal longitudinal trachea (*d. lt*), on each side of the thorax, lying near the digestive tract and connecting the branches from each of the three spiracles (sp_1, sp_2, and sp_3). The size and relationships of this trachea are such as to indicate that it may be only an enlarged anastomosis of the branches from the different spiracles. In adult cockroaches the intra-segmental portions of this longitudinal trachea become enlarged to form air sacs.

The former statement that the wing tracheæ of cockroaches are connected with the longitudinal tracheæ of the thorax has not been confirmed. (Comstock and Needham, *Am. Nat.* xxxii, p. 88). As the drawing shows, the basal connections of the wing tracheæ and the dorsal longitudinal tracheæ are quite separate.

The basal connections of the wing tracheæ in a nymph of Pteronarcys, Order Plecoptera.—The conditions of the wing and leg tracheæ in the stone-flies (Fig. 19) is somewhat complicated by the presence of tracheal gills but the relationships are quite generalized. The typical Y-shaped leg tracheæ are present in both cases, but in the case of both legs the posterior stem (*ps*) is connected with a trunk leading from the spiracle to the tracheal gill (*gt*). The cubito-anal wing tracheæ (*cu-a*) have diverged from the leg tracheæ until they have attained independent origins.

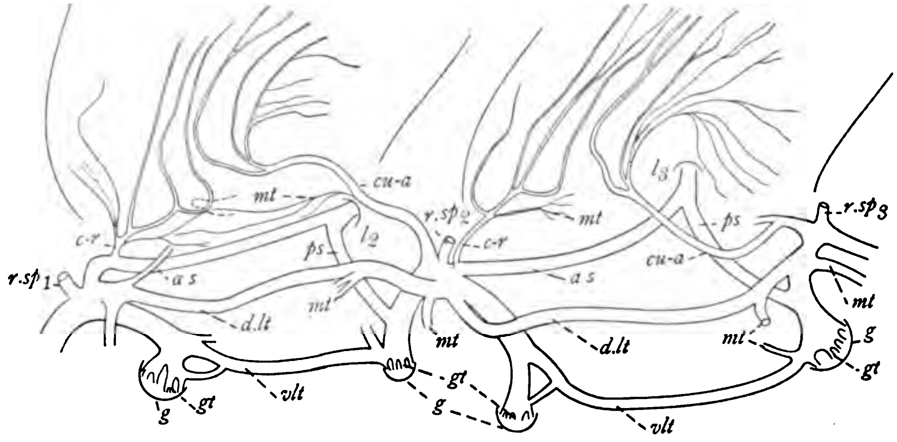

Fig. 19.—The basal connections of the wing tracheæ of *Pteronarcys*. Dorsal view.

The conditions of the anterior branches to the legs and wings have not been modified and the wing trachea (*c-r*) arises in common with the anterior stem of the leg trachea (*as*).

The dorsal longitudinal trachea (*d. lt*) is well developed but it will be noticed that it has no direct relationship to the wing tracheæ.

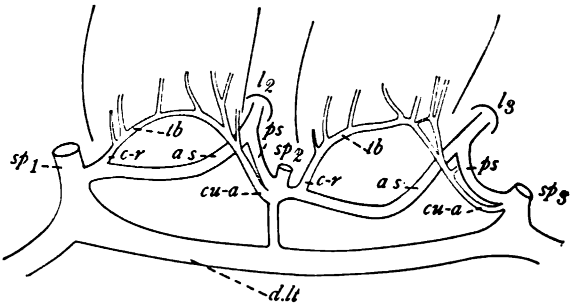

Fig. 20.—The basal connections of the wing tracheæ of *Chauliodes*. Dorsal view.

The basal connections of the wing tracheæ of Chauliodes, Order Neuroptera.—The wing tracheæ of *Chauliodes* (Fig. 20) represent no great deviation from the typical condition. It is interesting to note that the cubito-anal trachea (*cu-a*) and the posterior stem of the leg trachea (*ps*) are separated at their bases in both cases and that the costo-radial tracheæ (*c-r*) and the anterior stems to the legs (*as*) are connected for only a short distance. It would seem that the tracheæ to the wings are almost at the point of being separated from those of the legs, in this form.

The longitudinal trachea (*d. lt*) is well developed yet it does not seem to be in any way connected with the wing tracheæ.

The basal connections of the wing tracheæ of Antheræa roylei, Order Lepidoptera.—Three pupæ of the Lepidoptera were dissected, *Actias luna*, *Samia cecropæa*, and *Antheræa roylei*. Any of the three might have been used equally well for the conditions of the tracheæ are the same in all of them. In the mesothorax (Fig. 21) there seems to have been no modification from the typical condition, but in the metathorax the cubito-anal trachea (*cu-a*) and the posterior stem of the leg trachea (*ps*) are just separate from each other at their bases.

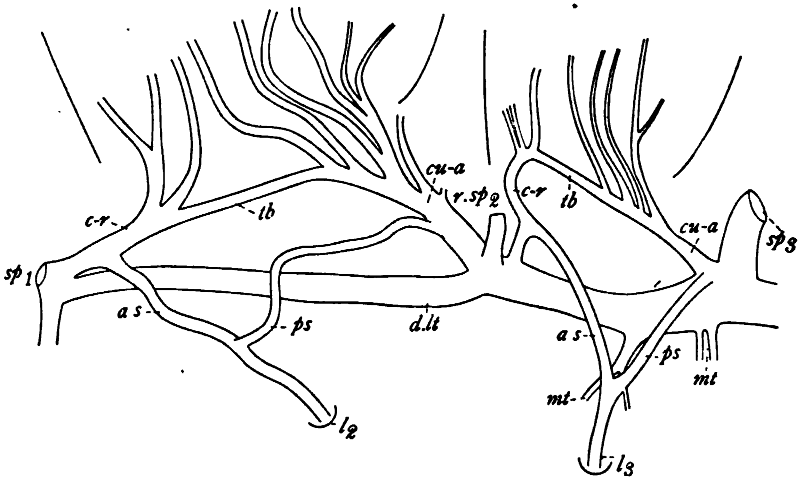

Fig. 21.—The basal connections of the wing tracheæ of *Antheræa*. Side view.

The dorsal longitudinal trachea (*d. lt*) is present but has no connection with the wing tracheæ. The metathoracic spiracle is absent but is represented by the trunk of the rudimentary spiracle ($r.\ sp_2$) with which the tracheæ have retained their typical relationships.

The thoracic tracheæ of *Antheræa perni* have been described and figured by Enderlein (*Zoologische Jahrbucher*, 1902; vi.).

This author figures tracheæ to the mesothoracic leg as a single stem arising from the spiracular trunk of the mesothorax and the leg trachea of the metathorax as also single and arising from the costo-radial trachea of the mesothorax. The conditions of the tracheæ seem to be so constant in representatives of this order which have been studied that it would seem very improbable that there should be such a great difference between two members of the same genus as Enderlein's figure would indicate.

The basal connections of the wing tracheæ of a notonectid nymph, Order Hemiptera.—The costo-radial tracheæ (Fig. 22 *c-r*) arise from the anterior stem of the leg tracheæ (*as*). The bases of the cubito-anal tracheæ (*cu-a*) have diverged from the posterior stems of the leg tracheæ (*ps.*) and have come to arise in common with muscle tracheæ (*mt*) which pass to the median part of the body. The conditions of the wing tracheæ are, however, so near the typical that there is no difficulty in understanding the relationships.

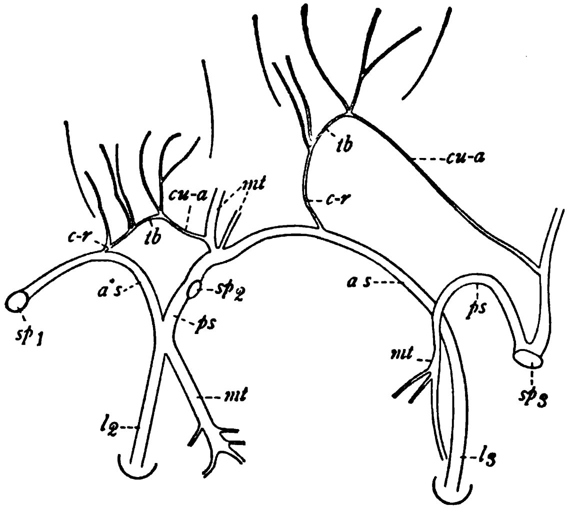

Fig. 22.—The basal connections of the wing tracheæ of a notonectid nymph. Side view.

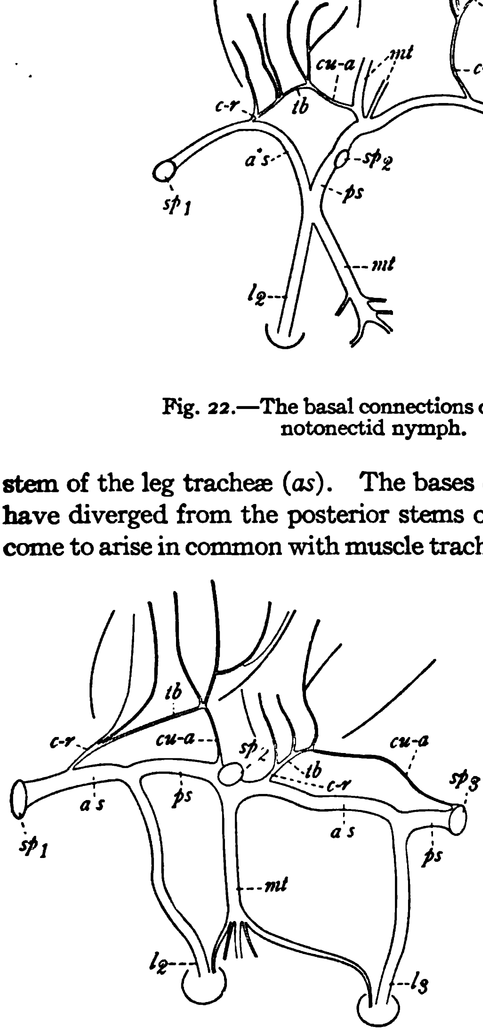

Fig. 23.—The basal connections of the wing tracheæ of a corisid nymph. Side view.

The leg tracheæ are modified to a greater extent. In the meso-thorax the anterior and posterior stems to the leg (*as* and *ps*) unite to form the typical Y-shaped leg trachea and at their point of union give off a large muscle trachea (*mt.*). The posterior stem of the leg trachea in the metathorax (*ps*,) lies laterad of the anterior stem (*as*) at their point of union and the muscle trachea (*mt*) appears to be a continuation of the posterior stem of the leg trachea (*ps*).

The basal connections of the wing tracheæ of a corisid nymph, Order Hemiptera.—The two tracheal stems to the wings (Fig. 23, *c-r* and *cu-a*) have retained their typical relationships in this form, but the cubito-anal trachea (*cu-a*) to the hind wing is so small at its base that it is followed with difficulty. The anterior and posterior stems of the leg tracheæ (*as* and *ps*) have attained an almost horizontal position, giving the leg tracheæ a T-shape. However, the relationships between the wing and leg tracheæ have remained typical.

The basal connections of the wing tracheæ of a Lethocerus nymph, Order Hemiptera.—The tracheæ leading to the wings are, of themselves, rather typical save for the divergence of the costal trachea (Fig. 24, *c*) from the costo-radial trachea (*c-r*) of the front wing. The relationships of the leg and wing tracheæ at first seem quite puzzling but if conditions are compared with those found in notonectids and corisids the explanation seems rather simple. It is quite evident that a "T" shaped trachea similar to that found in the corisid nymph has been modified by the posterior migration of the main trunk to the leg which has resulted in the lengthening of the anterior stem (*as*) and shortening of the posterior stem (*ps*) which results in the practical obliteration of the latter.

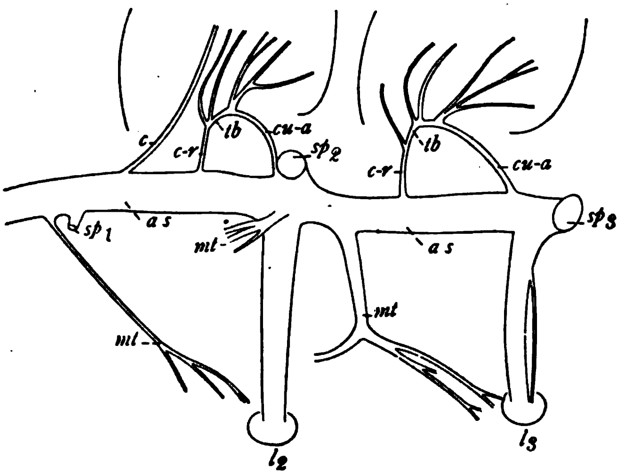

Fig. 24.—The basal connections of the wing tracheæ of *Lethocerus*. Side view.

The horizontal trunk leading from the mesothoracic spiracle (sp_1) to the metathoracic spiracle (sp_2) is, therefore, the anterior stem of the leg trachea (*as*) and the posterior stem of the leg trachea has disappeared. The costo-radial trachea (*c-r*) has its typical origin with the anterior stem of the leg trachea (*as*) altho it diverges from the latter some distance posterior to the typical position, and the costal trachea (*c*) has an independent origin. The condition of the tracheæ of the metathorax is similar to that of the mesothorax except that the costal trachea (*c*) has retained its typical position and the cubito-anal trachea (*cu-a*) has moved slightly forward and might almost be said to arise from the anterior stem of the leg trachea (*as*) in the absence of the posterior stem from which it typically arises.

The basal connections of the wing tracheæ of Monohammus, Order Coleoptera.—The wing tracheæ of the Coleoptera have retained their original relationships to the spiracular trunks but there is a modification of the leg tracheæ. Both of the posterior stems of the leg tracheæ (Fig. 25, *ps.*) are split nearly to their basal connections and they are entirely independent oh the cubito-anal tracheæ (*cu-a*). The anterior stem of the leg tracheæ (*as.*) of the metathorax is very slender but it has retained its original connection with the costo-radial trachea (*c-r*). In the mesothorax the anterior stem of the leg trachea is entirely absent.

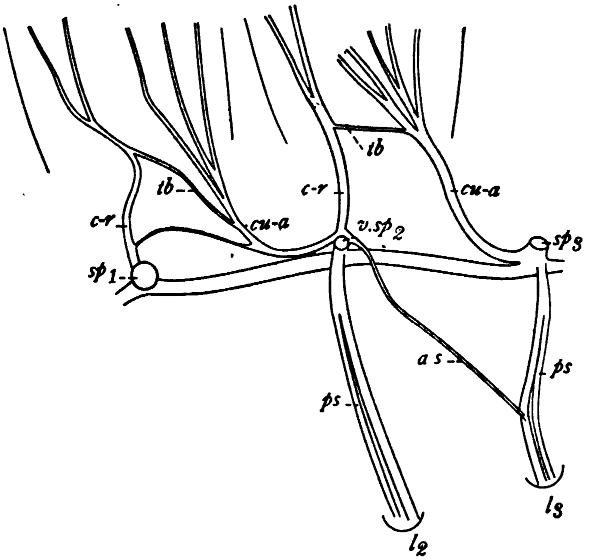

Fig. 25.—The basal connections of the tracheæ of the wings of *Monohamus.* Side view.

The longitudinal trachea is well developed and the position of the metathoracic spiracle, which is absent, is indicated by the spiracular trunk (*v.* sp_2). None of these conditions seem to have modified the original relationship of the wing tracheæ to the spiracular trunks.

The basal connections of the wing tracheæ of Bittacomorpha, Order Diptera.—The connections in this form are rather generalized and even tho the hind wing is absent the halter receives tracheæ which have all the relationships that the tracheæ to the wing would have (Fig. 26). There is a tendency toward the reduction of the cubito-anal tracheæ which are very small and are followed with difficulty in dissection. The tracheæ to the legs are unmodified except for the shortening of the anterior stem (*as*) to the hind leg.

EXAMPLES OF SPECIALIZATION BY REDUCTION

The basal connections of the wing tracheæ of Rhyacophila, Order Trichoptera.—The wing tracheæ of *Rhyacophila* are greatly reduced and the basal connections are correspondingly specialized. The thorax is specialized in that there are marked intersegmental depressions on the sides, within which the rudimentary spiracles are found. However, the connections to the legs have retained their primitive condition.

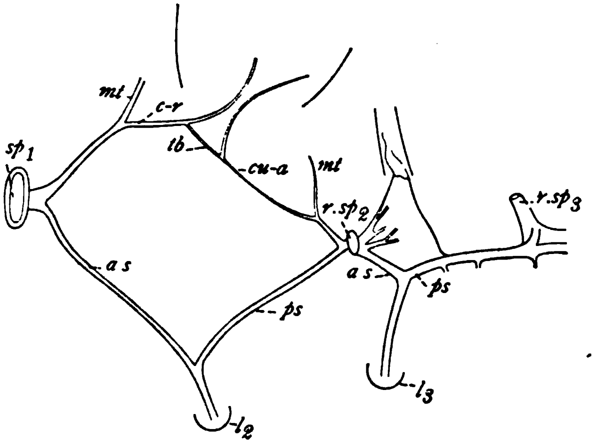

Fig. 26.—The basal connections of the tracheæ of the wings of *Bittacomorpha*. Side view.

The wing tracheæ of each wing appear to arise as two trunks which connect indirectly with the mesothoracic spiracular trunk (Fig. 27, sp_1) in the case of the front wing, and the metathoracic spiracular trunk (sp_2) in the case of the hind wing. The anterior trunk to each wing arises in common with the anterior stem of the leg trachea and is undoubtedly the costo-radial trachea (*c-r*).

The cubito-anal trachea of each wing (*cu-a*) arises in its typical position near the spiracle which normally supplies it with air. But owing to a cephalization of its air supply which results in this trachea receiving the greater part of its air by the way of the transverse basal trachea (*tb*) its course becomes greatly modified and the proximal portion of it greatly reduced. This results in that part of it beyond the point of union with the transverse basal trachea appearing to be a continuation of that trachea.

There has been developed a small accessory longitudinal trachea (*a-dt*) which arises with the transverse basal trachea near the spiracular trunk and extends parallel to the dorsal longitudinal trachea (*d. lt*). Its only connection with the wing trachea is at its point of origin.

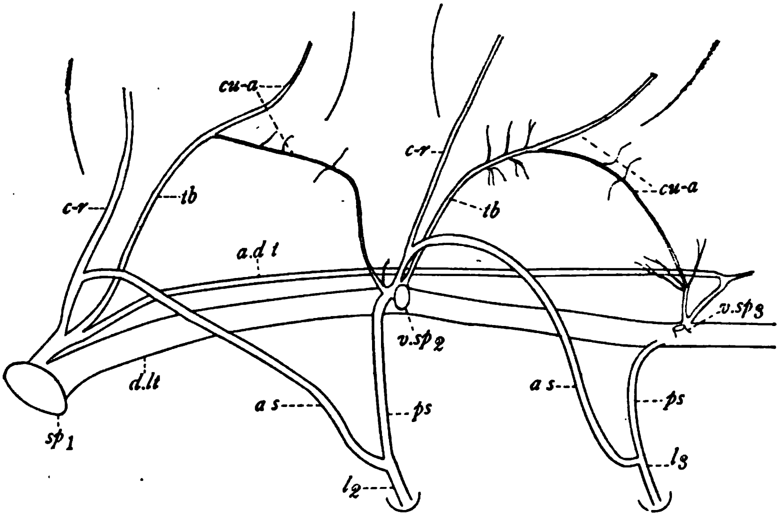

Fig. 27.—The basal connections of the tracheæ of the wings of *Rhyacophila*. Side view.

The basal connections of the wing tracheæ of an unknown genus (*Limnophilidæ*), *Order Trichoptera.*—This form illustrates an interesting step in the reduction of the tracheæ to the wings. (Fig. 28). In the hind wing both

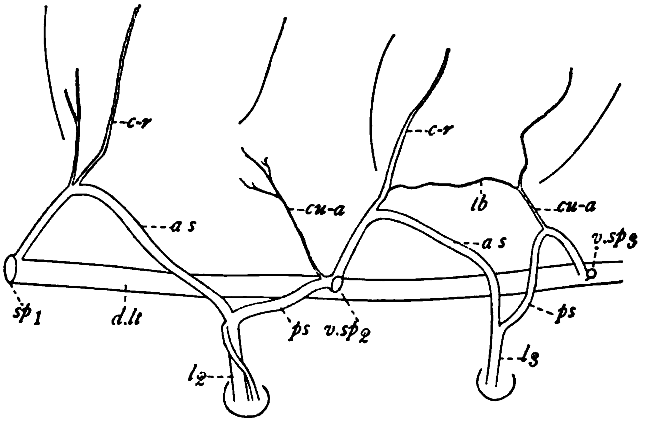

Fig. 28.—The basal connections of the tracheæ of the wings of unknown genus of *Trichoptera*. Side view.

the costo-radial (*c-r*) and cubito-anal tracheæ (*cu-a*) are present altho the latter is very small as is also the transverse-basal trachea (*tb*). In the front wing the cubito-anal trachea and the transverse basal trachea are absent. However the reduced cubito-anal trachea (*cu-a*) is present in the thorax with its typical connections except that it fails to reach the wing. The leg tracheæ have the typical connections.

The basal connections of the wing tracheæ of Stenophylax, Order Trichoptera.—The cubito-anal tracheæ (Fig. 29) do not reach the wing in either case in this form altho their vestiges are present in the thorax (*cu-a*) and both have their typical connections with the posterior stems of the leg tracheæ (*ps*). In both cases the costo-radial tracheæ (*c-r*) have their typical connections except that the transverse basal tracheæ are entirely absent.

The basal connections of the wing tracheæ of a nymph of Epeorus. Order Ephemerida.—The wing tracheæ of Mayflies are highly specialized and there is a marked cephalization of the flight function in this order. Morgan in a paper on the wings of May-flies (Morgan, Anna H. Homologies of the wing veins of the May-flies, Annals, Ent. Soc. Amer. 1912, v. 5, p. 89–105), concluded that the wing tracheæ of *Epeorus* represented one of the more generalized conditions. For this reason *Epeorus* has been used for the study of the basal connections of these tracheæ.

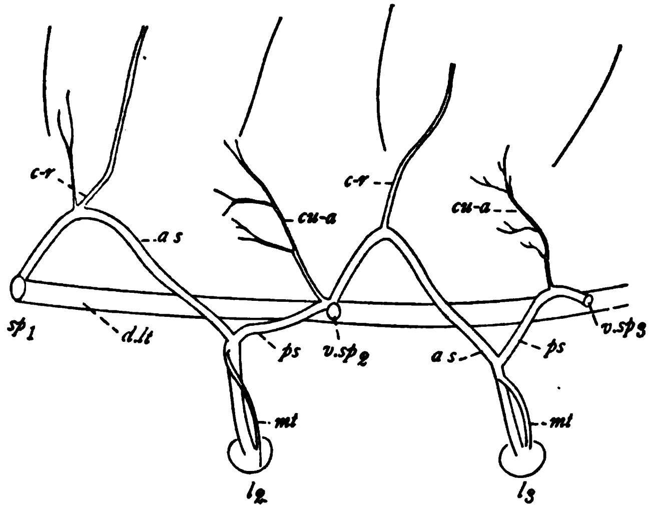

Fig. 29.—The basal connections of the tracheæ of the wings of *Stenophylax*. Side view.

The anterior tracheæ to each leg and wing have retained their primitive conditions (Fig. 30); the anterior stem of the leg tracheæ (*as*) and the costo-radial trachea (*c-r*) to the wing have a common origin in each case. However the posterior connections to the wings and legs have been greatly reduced. The portion of the cubito-anal trachea (*cu-a*) proximal to its union with the transverse basal trachea (*tb*) is absent except for a short vestige in the front wing. This short vestige extends proximally from the union of the transverse basal trachea (*tb*) and the cubito-anal trachea (*cu-a*) and connects with a small accessory trachea which leads anteriorly to the costo-radial trachea (*c-r*). The remainder of the cubito-anal trachea which Morgan had suspected to be present, was not found in any of the specimens dissected. Even this small vestige was found to be absent in the hind wing.

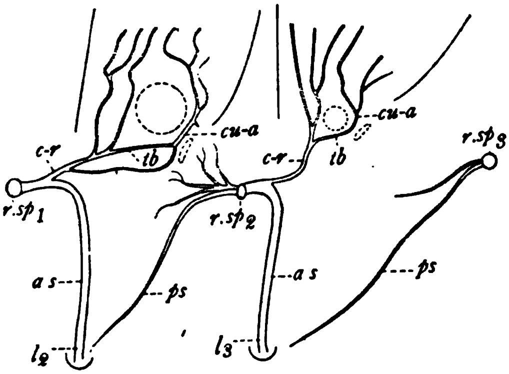

Fig. 30.—The basal connections of the tracheæ of the wings of *Epeorus*. Side view.

The posterior stems of the leg tracheæ (*ps*) are represented by slender tracheæ which enter the coxæ in the typical position for the posterior stems of the leg tracheæ but their connections with the anterior stems (*as*) are very slight and seem to be lacking in some cases. It is very evident that the posterior tracheæ to the legs are at the point of being lost in this form.

There is a saucer shaped disc, which has been indicated by a dotted line in the figure, between the cubito-anal and costo-radial groups of tracheæ in each wing. There is also a well developed apodeme, represented by a dotted line, just posterior to the union of the cubito-anal trachea (*cu-a*) and the transverse basal trachea (*tb*) in each wing. The influence of these structures upon the tracheæ of the wings will be taken up in the latter part of this paper.

The basal connections of the wing tracheæ of Chirotonetes nymph, Order Ephemerida.—The conditions of the basal connections of the wing tracheæ of *Chirotonetes* are more easily understood after having studied the conditions in *Epeorus*. In *Chirotonetes* (Fig. 31) the anterior tracheal connections to the legs and wings have retained their primitive condition but the posterior connections are entirely absent. Small muscle tracheæ, somewhat resembling the typical posterior connections, were found but their former connections have been entirely lost and the cephalization of the air supply to the wings is complete.

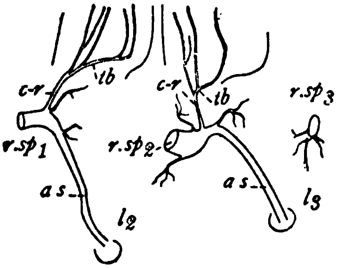

Fig. 31.—The basal connections of the tracheæ of the wings of *Chirotonetes*. Side view.

The basal connections of the wing tracheæ of Apis mellifica, Order Hymenoptera.—The pupa of a drone honey bee was used for the study of the trachea of this form because of its large size. The highly specialized bee has specialized tracheal conditions but a study of the figure will recall the conditions in the more generalized insects. The Y-shape of the leg tracheæ is as striking in the metathorax of the honey-bee as in the diagram of the typical condition (Fig. 32). In the mesothorax the anterior stem to the leg (*as*) is greatly elongated and extends dorsally to its connection with the costo-radial (*c-r*) branch to the wing and then passes ventrally into the leg. The posterior stem (*ps.*) to the mesothoracic leg ($l._2$) is united with the anterior stem (*as*) to the metathoracic leg a short distance from the spiracular trunk. The spiracular trunk leading to the vestige of the metathoracic spiracle (*v. sp*$_2$) is very long.

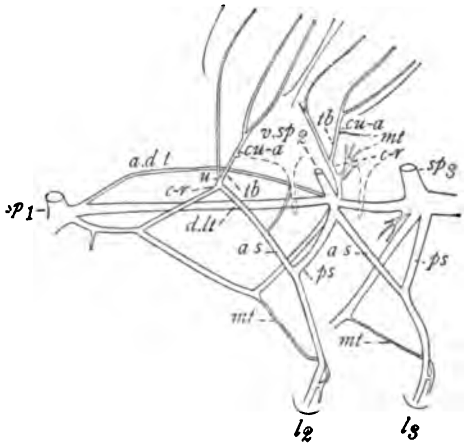

Fig. 32.—The basal connections of the tracheæ of the wings of *Apis*. Side view.

The tracheæ leading to the muscles of the coxae (*mt*) are well developed, and as shown in the figure, are united much like the leg tracheæ with which they actually connect. But these muscle tracheæ lie deep within the thorax and are relatively much smaller than the true leg tracheæ.

The branches to the wings exhibit the greatest specialization. In the case of both wings the air supply comes entirely from the spiracle anterior to the wing, for there is no connection with the spiracle posterior to the wing. A short distance distad from the union of the two branches to the front wing there will be noticed a slight projection from the tracheæ. This projection is in such a position that it is highly suggestive of a vestige of the former cubito-anal trachea which extended from this point to the base of the metathoracic spiracular trunk. In a similar position on the trachea leading to the hind wing there are a few tracheal branches which may have a significance similar to that which has been ascribed to the projection on the trachea leading to the front wing. If these structures represent the vestiges of the cubito-anal tracheæ leading to the spiracular trunks, the part of the tracheæ between these structures and the union of the tracheæ (*u*) must represent the transverse basal trachea and the remainder of the posterior branch must represent the distal part of the cubito-anal trachea (*cu-a*).

EXAMPLES OF SPECIALIZATION BY ADDITION

The basal connections of the wing tracheæ of a nymph of Melanoplus sp., Order Orthoptera.—The dissection of an acridid nymph is rather difficult because of the many tracheal branches and air sacs in the thoracic region. The minor branches and the air sacs were removed in the course of the dissection and the figure is a camera-lucida drawing of the tracheæ with which this paper is concerned together with the more important minor branches.

The tracheal connections are modified to a certain extent but the conditions are easily explained (Fig. 33). The point of union of the costo-radial trachea (*c-r*) and the anterior stem of the leg trachea (*as*) has moved dorsad in both cases. In the mesothorax the anterior stem to the leg arises from the spiracular trunk (sp_1) and goes dorsad to the point where the costo-radial trunk (*c-r*) is given off and then it passes ventrad to meet the posterior stem (*ps*) thus forming the usual Y-shaped trachea to the leg. It will be noticed that the posterior stem is the larger of the two.

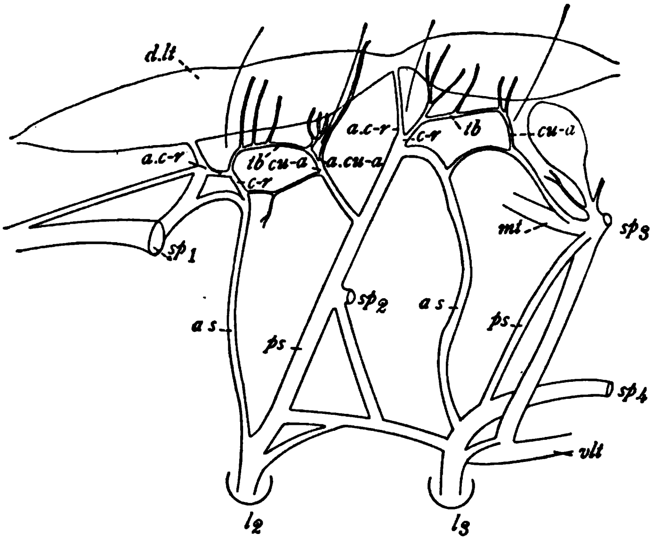

Fig. 33.—The basal connections of the tracheæ of the wings of *Melanoplus*. Side view.

From the costo-radial trachea (*c-r*) of the front wing there is an accessory trachea (*a. c-r*) which connects with the saclike dilated dorsal longitudinal trachea (*d.lt*). The base of the cubito-anal trachea (*cu-a*) has fused with the anterior stem (*as*) to the metathoracic leg to form a common trunk extending dorsad for a short distance from the metathoracic spiracle. The cubito-anal trunk (*cu-a*) to the front wing has an accessory tracheal connection (*a. c-a*) which passes mesad, just dorsad of the dorsal longitudinal trachea (*d. lt*), to anastomose with its fellow of the opposite side.

The changes in the costo-radial trachea to the hind wing have been similar to those to the front wing. The anterior tracheal stem to the leg (*as*) forms a common trunk with the cubito-anal trachea of the front wing, as has just been described, and then it continues dorsad, in common with the costo-radial trunk (*c-r*) of the hind wing, until it becomes independent of the wing trachea and passes ventrad to unite with the posterior stem of the leg trachea (*ps*).

The costo-radial trachea of the hind wing also has an accessory connection (*a. c-r*) with the dilated dorsal longitudinal trachea (*d. lt*). The cubito-anal connection (*cu-a*) is unmodified except for a small accessory connection between it and the anterior stem of the leg trachea (*as*), similar to a connection found in the mesothorax.

The posterior stem (*ps*) of the trachea to the metathoracic leg (l_3) is small and has new relationships at its point of entrance into the specialized hind leg. The descriptions of the leg trachea in the metathorax, which have given rise to these new relationships involving the second abdominal spiracle, belong more properly to the last part of this paper and their discussion will be postponed for the present.

The basal connections of the wing tracheæ of Anax and Lestes, Order Odonota.—The tracheation of *Plathemis lydia* was described and figured by G. G. Scott (*Biological Bulletin* 1905, ix: 341–354). The author described the tracheæ of the wing as arising from a loop, the anterior trachea of the loop arising from the dorsal longitudinal trachea and the posterior trachea, in the case of the mesothorax, arising from the short transverse connective in such a way that the two posterior tracheæ of the fore wings originate side by side. The tracheation of the hind wings is described as similar to that of the fore wings except that the anterior trachea arises from the spiracular trunk near the dorsal longitudinal trachea and the posterior trachea is described as originating directly from the dorsal longitudinal trachea.

R. J. Tillyard (*Proceedings of the Linnean Society of New South Wales*, 1914, xxxix, pt. 1, p. 163–216, pl. xi–xiii) made a study of Odonata nymphs using transmitted light to distinguish the tracheæ. His description is said to embody the results obtained from the study of both the Anisoptera and the Zygoptera and a diagram of the lateral view of the thorax is given to show the connections of the wing tracheæ. This author describes one tracheal branch to each leg and one trachea, arising from the dorsal longitudinal trachea, as entering each wing pad from the anal end, forming a loop from which the wing tracheæ arise, and passing out of the wing pad at the costal end as a fine threadlike trachea which connects with the leg trachea of the same segment.

Tillyard's description and figure differ from those of Scott in that the former author has the anterior wing tracheæ connecting with the leg tracheæ and the posterior wing tracheæ connecting with the longitudinal trachea, while the latter author has the anterior trachea of the fore wing connecting with the dorsal longitudinal trachea and that of the hind wing connecting with the spiracular trunk near the dorsal longitudinal trachea.

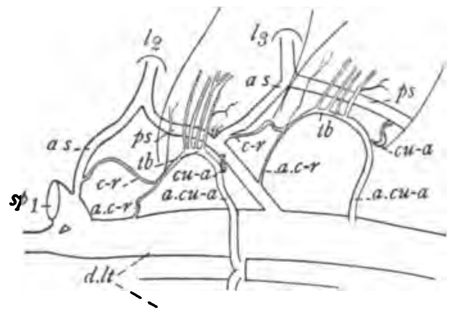

Fig. 34.—The basal connections of the tracheæ of the wings of *Anax*. Dorsal view.

The posterior trachea to the wings is said by him to connect with a transverse connective, in the case of the fore wing, and with the dorsal longitudinal trachea in the case of the hind wing.

The figures accompanying this paper are the result of numerous dissections and show the conditions in a representative of each of the two suborders (Figs. 34 and 35). There are two tracheæ entering the front of each wing pad, the usual costo-radial trunk (*c-r*) connecting with the anterior stem of the leg trachea (*as*) and accessory costo-radial trunk (*a. c-r*) connecting with the dorsal longitudinal trachea (*d. lt*), in the case of the front wing, and with the trunk to the vestigial metathoracic spiracle, in the case of the hind wing. It is probable that Tillyard has seen the costo-radial trachea in studying the lateral view of the thorax while Scott has seen the accessory costo-radial trachea in his study of the dorsal view of the thorax, which he figures.

There are likewise two posterior tracheæ to each wing pad. The cubito-anal tracheæ (*cu-a*)of both wings are vestigial and are made out with some difficulty but they have retained their original connections with the posterior stems of the leg tracheæ. The accessory cubito-anal tracheæ (*a. cu-a*) are much the larger; the one to the fore wing arises from the transverse connective which lies

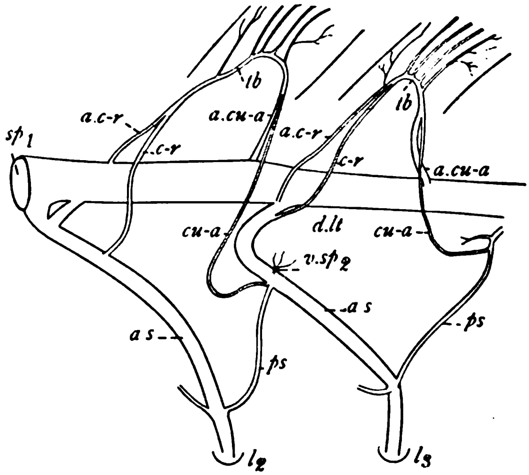

Fig. 35.—The basal connections of the tracheæ of the wings of *Lestes*. Side view.

between the two dorsal longitudinal tracheæ (*d. lt*) as described by Scott (*l. c.*) and the one to the hind wing arises from the dorsal longitudinal trachea. It will be noticed that in the side view of *Lestes* (Fig. 35) the connection of the accessory cubito-anal trachea (*a. cu-a*) of the mesothorax with the transverse connective cannot be seen for it is hidden by the dorsal longitudinal trachea (*d. lt*). The vestige of the true cubito-anal trachea (*cu-a*) has doubtless been overlooked by both of the former authors.

THE INFLUENCE OF THORACIC STRUCTURE ON THE CONNECTIONS OF THE WING TRACHEÆ

The main tracheæ of insects lie in the spaces of the body allowing for the free passage of air thru their lumina. Their flexibility is a necessity for tracheæ entering the appendages of the body must bend readily when these structures are moved and it is all important that the flexible tracheæ should avoid contact with any structure which might at any time bring pressure to bear upon their walls and interfere with the free passage of air. The course of the tracheæ to the wings might be expected to be direct but at the same time the avoidance of rigid structures, such as those concerned with the movement and articulation of the wings, among which the tracheæ must pass, would seem to be an important factor in determining their course.

The material presented in this paper affords many examples of altered courses of tracheæ which seem to be due to peculiarities of thoracic structure. In the wing of the Mayfly, *Epeorus*, (Fig. 30) a simple example may be found. There is a saucer-shaped disc, which has already been referred to as lying between the medial, cubital, and transverse basal tracheæ, and which has been indicated in the drawing by a dotted line, around which the tracheæ pass. This disc with its two chitinous walls of such convexity would undoubtedly be a great obstacle to the passage of air if the tracheæ crossed it rather than encircled it as they do, altho the latter course of the tracheæ is the longer.

The case of the stone fly, *Pteronarcys* (Fig. 19), presents an example of the modification of the medial trachea (*m*) which is very suggestive. The medial trachea (*m*) will be noticed to arch caudad toward the cubito-anal group of tracheæ and altho there is no transverse basal trachea the medial trachea might, from its position, be considered to be midway between the costo-radial and cubito-anal groups of tracheæ. The examination of a nymph which is nearly ready to emerge will show a strong process, evidently the wing process, (indicated by a dotted line in the drawing) projecting between the radial (*r*) and medial (*m*) tracheæ to articulate with an over-lying articular sclerite, evidently the second axillary sclerite. Here again it seems very clear that the course of a trachea is modified from the most direct route by a mechanical obstruction. Moreover this case is very significant for the cause of the migration of the medial trachea along the transverse basal trachea, as stated in the introduction, was one of the problems which prompted this research.

Modifications of the thorax which would result in the posterior migration of the wing process would also result in the posterior migration of the base of the medial trachea. Likewise a cephalization of the wing would bring the cubito-anal group of tracheæ nearer the medial trachea, if the wing process remained in its original position and did not allow the medial trachea to move cephalad with the rest of the structures of the wing.

The consideration of the relationships of thoracic peculiarities andthe modifications of the tracheæ to the wings may profitably be extended to the more general conditions. The insects considered in this paper have been divided into three groups: those with generalized connections of the wing tracheæ, those with reduced connections of the wing tracheæ, and those in which the connections of the wing tracheæ have been specialized by the addition of new connections. In the group where the conditions of the tracheal connections are generalized the thoracic structure is also generalized. The examples of the Blattidæ among the Orthoptera, the Plecoptera, the Neuroptera, the Lepidoptera, and the others are quite generalized, while the Coleoptera and Hemiptera are mentioned both for their somewhat generalized wing connections and for the reduced connections to the legs, which latter condition is accompanied by the oblique position of the lateral sclerites of the thorax.

Among the insects with reduced connections of the wing tracheæ there are many varieties of thoracic structure illustrating several lines of specialization. It is not the purpose of this discussion to enter into the details of so complex a region as the thorax or to attempt to ascribe all the modifications of the connections of the wing tracheæ to the peculiarities of thoracic structure alone, but rather to call attention to the fact that reduced wing tracheæ occur in the insects that have a specialized thorax. In the drawings of the Ephemerida (Figs. 30 and 31) and the Hymenoptera (Fig. 32). apodemes are represented by dotted lines just posterior to each wing. These apodemes may be studied in insects which are about to emerge from the pupal state and from their position it seems very probable that they obstruct the course of the cubito-anal tracheæ and eventually lead to their reduction and the consequent cephalization of the air supply to the wings.

The last group of insects, those with additional tracheal connections to the wings, includes the Odonata (Figs. 34 and 35) and the jumping Orthoptera (Fig. 33). These two groups of insects are peculiar in that their nymphs have their wing pads flexed dorsally, approximating the mid-dorsal line. Such a position of the wingpads favors the enlargement of any median tracheal connections such as the accessory connections to the wings (*a. c-r*) and (*a. cu-a*) because the wingpads are drawn so close to the dorsal longitudinal tracheæ. On the other hand, the original tracheæ (*cu-a* and *c-r*) must be greatly elongated and no doubt are obstructed by apodemes along their new path, especially in the case of Odonata.

The accessory cubito-anal trachea (*a. cu-a*) of the Odonata is much larger than the reduced cubito-anal trachea (*cu-a*) and is also larger than either of the anterior tracheal connections (*c-r* and *a. c-r*), each of which is about half its size. The fact that the two anterior tracheæ have had their courses altered by the change in form is probably the cause of their reduction.

Some of the most interesting correlations between thoracic structure and tracheal conditions are to be found in the study of the leg tracheæ and the analogy with the conditions of the wings is most instructive in the consideration of their tracheæ. In the Coleoptera (Fig. 25) where the thorax is oblique and the legs have moved caudad, the anterior stem (*as*) to the mesothoracic leg (l_2) is absent and the anterior stem to the metathoracic leg (l_3) is small while both of the posterior stems are large.

The Hemiptera (Figs. 22, 23, and 24), which have a thorax like that of the Coleoptera, also have modified conditions of the leg tracheæ which are most marked in the Belostomidæ (Fig. 24) where there is a single stem of the leg trachea, due to the posterior migration of the main leg trachea which results in the obliteration of the posterior stem and the elongation of the anterior stem of the trachea.

The Odonata present a thorax which is oblique in the opposite direction from the examples mentioned above, for the legs have moved cephalad. This skewness of the thorax in the Odonata was studied by Needham and Anthony (*Journal of the New York Entomological Society*, 1903, xi: 117–125) and the angle formed between the perpendicular and the humeral angle was found to vary from 21 degrees in some of the Aeschninæ to 71 degrees in certain Agrioninæ. This furnishes a series of modifications in which the tracheæ may be studied and it has been found by a study of a series of nymphs that the proportionate size of the anterior stem of the leg trachea varies in direct proportion to the size of the angle of the thorax, while the size of the posterior stem of the leg trachea varies in inverse proportion to the size of the thoracic angle. The thoracic angle of *Anax junius* (Fig. 34) is 27 degrees and the posterior stem of the leg trachea (*ps*) is slightly larger than the anterior stem (*as*). *Lestes* (Fig. 35) has a thoracic angle of 66 degrees and the posterior stem of the leg tracheæ (*ps*) is very small while the anterior stem (*as*) is comparatively large.

In this connection it is interesting to note that Tillyard (l. c. p. 205) entirely overlooked the posterior stem of the leg trachea in his figure of *Austrolestes*. The Odonata, therefore, with their highly modified thorax and greatly altered tracheæ to both the wings and legs, present the best example of the correlation between thoracic structure and the tracheal connections.

The jumping Orthoptera (Fig. 33) have the tracheation of the hind leg greatly modified in that a part of the tracheæ come from the second abdominal spiracle. This is a condition which has been met with nowhere else and is undoubtedly due to the great development of the hind leg and its intrusion into the abdominal region.

THE COMPARATIVE VALUES OF THE AIR SUPPLIES TO THE TWO PRINCIPAL TRACHEÆ OF THE WINGS

The value of the air supply of the wing tracheæ has been suspected of being the cause of some of the tracheal modifications of the wings. This theory has been mentioned in the introduction of this paper and it has been given some study by Tillyard (l. c. p. 207–218). This author has made a study of the Odonata where the basal connections of the tracheæ are most highly modified. The author has formulated a theory, as the result of his work, which reads as follows:

"The peculiarities shown by the wing-venation of the Odonata, as contrasted with that of other insects, are due primarily to the aquatic habits of the larvæ; whereby, thru the development of rectal or caudal breathing, the oxygen-supply of the developing wing is carried from the posterior end of the body, and enters the wing-base at its anal end."

The invasion of the area of the radial sector by the medial trachea is accounted for by the fact that the medial trachea is nearer the air supply than the radial trachea. Several other modifications are ascribed to the same cause.

The Odonata would seem a very unfavorable order to use in the study of the comparative values of the air supplies to the wings because the conditions are so highly specialized. A better understanding of the subject may be had by returning to the typical condition of the tracheal connections and following the various lines of development.

Each wing typically receives air from two spiracles and the metathoracic spiracle (Fig. 17, sp_2) supplies the cubito-anal portion of the front wing and the costo-radial portion of the hind wing. It may be assumed that the three typical sources of air supply are equal. The Lepidoptera (Fig. 21) have the tracheal connections to the wings very generalized but the metathoracic spiracle (*r. sp*) is rudimentary in the pupa. This would seem to make the air supply to the cubito-anal portion of the front wing and the costo-radial portion of the hind wing inferior to the others and the tracheation of the two wings should be quite different. On the other hand the tracheæ seem to have been unmodified and to have retained their typical relationships.

It is difficult to apply the air-supply theory to the case of the honey-bee for the hind wing has lost its cubito-anal connection which was with the functional first abdominal spiracle (Fig. 32 sp_3) and has retained its costo-radial connection (*c-r*) with the trunk of the vestigial metathoracic spiracle (*v. sp_2*). The posterior wing has, therefore, forsaken the best source of air supply and retained a connection with a trunk which no longer has an opening to the exterior.

In all the cases where the wing tracheation has been reduced it is the cubito-anal trachea which has been lost. If the air supply is the factor causing the one connection to be lost and the other connection to be retained it is not easy to understand how it operates in the case of the metathoracic spiracle, for here the cubito-anal trachea to the front wing is lost and the costo-radial trachea to the hind wing is retained.

To return to the case of the Odonata where the air-supply theory seems to find its best support, the posterior connection to the front wing should be considered. If the accessory cubito-anal trachea (Fig. 34, *a. cu-a*), which is enlarged, connected with the dorsal longitudinal connective (*d. lt*) as Tillyard (*l. c.*) thought, it would be favorable to the air-supply theory, but it connects with a small transverse connective between the two dorsal longitudinal tracheæ. This makes an indirect course for the air to follow in going to the wing and the condition would seem to be more easily explained as having arisen as an enlargement of a simple anastomosis of the accessory cubito-anal tracheæ of both sides, a condition found in *Melanoplus* (Fig. 33). The union of these tracheæ might easily have anastomosed with a transverse connective to form a course which later became enlarged because it was the least obstructed route for the air to follow to the wings.

It should be remembered that there are two anterior tracheæ leading to the wing pad (*c-r* and *a. c-r*), each of which is about half the size of the posterior trachea (*a. cu-a*) and the two together must supply about as much air to the wing as this posterior trachea does.

The condition of the leg tracheæ in the Odonata is very instructive in the study of the values of the air supplies in the thorax. The legs, like the wings, each have two tracheal connections which typically derive their air supply from the same sources as do the tracheæ to the wings. But in the Odonata the posterior stem of the leg tracheæ, which should offer the more direct course for the air to follow in passing to the legs from the gills at the posterior end of the body, is greatly reduced, when the thoracic angle is great, while the anterior stem with its less direct course is enlarged. This would indicate that the directness of the air supply has little to do with the modification of the leg tracheæ in the Odonata.

The belief that the migration of the medial trachea along the transverse basal trachea toward the cubito-anal group of tracheæ might be due to the better air supply to that group was referred to in the introduction of this paper. In view of the fact that the basal connection of the posterior group of tracheæ is the one to be lost in all cases where there is a reduction of the tracheal connections, it seems more reasonable to ascribe this migration of the medial trachea to peculiarities of thoracic structure, as has been done above.

The invasion of the area of the radial sector by the medial trachea in the Odonata was also referred to in the introduction as a condition which might be due to the better air supply of the cubito-anal trachea. In the Odonata the distance between the bases of the radial and medial tracheæ is so short that it would hardly seem that the medial trachea should be so modified as to invade the area of the radial trachea in order to save the air from passing so short a distance along the transverse basal trachea. The May-flies illustrate the same condition of the medial trachea invading the area of the radial sector, but here the connection of the cubito-anal trachea has been lost and the air supply of the wing has been completely cephalized so that the medial trachea is less favorably situated, with regard to the directness of the air supply, than is the radial trachea, the area of which it has invaded.

From all these considerations it would seem that the directness of the air supply is not an important factor in controlling the relationships of the tracheæ. However, the function of the tracheæ is to supply air and, even tho the surrounding structures may obstruct their way and cause them to become modified and adopt new and longer courses, they must still furnish an adequate supply of air to the tissues. The accessory cubito-anal tracheæ to the hind wings of the Odonata is a case where the least obstructed course for the tracheæ to follow is also the shortest course, but the majority of cases, such as the modified base of the medial trachea of the stonefly and the single trachea to the wing of the honey-bee connecting with the trunk of a vestigial spiracle, have seemed to have no regard for the distance which the air must pass in reaching the tissues, but they have all adopted the least obstructed course for the air to follow. The length of the tracheæ, therefore, does not seem to be the factor causing the modifications of structure, but rather a course for the tracheæ which is free from obstruction and which will allow for the passage of the air. Whether the air reaching the radial trachea comes from the costo-radial or cubito-anal trachea makes no difference to the tissues so long as the course of the radial trachea is unobstructed. The medial trachea, on the other hand, would not be expected to invade the area of the radial trachea simply because its base might be a millimeter or two nearer to the source of air supply any more than the radius should invade the area of the media in forms like the May-flies where the cubito-anal trachea has been lost.

CONCLUSIONS

The material upon which this discussion is based does not constitute an exhaustive study of this subject, for each order of insects presents an opportunity for more detailed research. However, there are certain points with